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RESEARCH ARTICLE

Beaver wetlands create a buzz and a flutter for pollinators

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Abstract

1. Beavers are second only to humans in their capacity to transform landscapes. Biodiversity responses to their habitat engineering activities are well studied but rarely so 'beyond the pond' despite habitat alteration commonly extending into more terrestrial environments. Potentially profound spillover effects on, for example, pollinator communities, may therefore be overlooked.
2. In this study, we compared plant communities, pollinator communities and plant–pollinator networks around beaver wetlands and human-created ponds. Specifically, we tested if these wetland types differ in terms of (1) plant species richness and community composition, (2) pollinator species richness and abundance, and the floral characteristics (number of species in flower and maximum flower coverage) to which pollinators respond and (3) specialisation of their plant-pollinator networks.
3. Plant composition but not species richness differed between the two wetland types. Beaver wetlands supported more ruderal and competitor indicator species, whereas human-created ponds had more stress tolerators.
4. Hoverfly richness (+29%), hoverfly abundance (+119%) and butterfly abundance (+45%) were higher in beaver wetlands, the former two being positively associated with number of species in flower and maximum flower coverage, and the latter with open habitats. Butterfly richness and both the richness and abundance of bees and moths showed no difference between wetland types.
5. Hoverflies were the dominant flower visitor in beaver wetlands and bees in human-created ponds, but network level specialisation did not differ significantly between the two wetland types.
6. *Synthesis and applications*. Our results show that beaver wetlands boost hoverfly richness/abundance and butterfly abundance and diversify foraging resources for pollinators while comparing favourably with human-created ponds for other pollinators. Support for beaver wetlands, in tandem with riparian buffers and pond margins, should therefore be advocated in agri-environment schemes to recognise the pollinator services they provide.

KEYWORDS
beaver, Diptera, plant–pollinator interactions, pollinator, pollinator network, pond, wetland

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1 | INTRODUCTION

Urgent implementation of novel habitat restoration techniques is required to reverse the ongoing catastrophic declines in pollinators (Cornelisse et al., 2025; Fox et al., 2023). As we reach midway through the UN Decade of Ecosystem Restoration 2021–2030, and the threats to pollinators (including direct habitat loss, climate change and extensive application of pesticides) continue unabated (Ganuza et al., 2022; Nath et al., 2023), implementation of proven solutions becomes increasingly critical (Cook et al., 2024).

Beavers (Eurasian beaver *Castor fiber* and North American beaver *Castor canadensis*) are nature's foremost freshwater ecological engineers, second only to humans in their capacity to transform landscapes. Ecosystem engineers, such as beavers, strongly influence abiotic conditions by modifying their habitat, which in turn can alter biological communities and the delivery of ecosystem functions, such as pollination (Byers, 2024; Romero et al., 2015). Engineering by beavers involves regular small to medium-scale spatial-temporal disturbances. This includes the impoundment of water through the construction of dams and canals, which alters the local hydrological regime and increases soil moisture (Hartman & Törnlöv, 2006; Hood & Larson, 2015). Beavers also selectively fell and browse riparian trees and graze on herbaceous vegetation, modifying the structure of the surrounding aquatic and terrestrial environment (Hyvönen & Nummi, 2008; Law et al., 2017; Zwolicki, 2025). Positive biodiversity responses to their habitat engineering activities (e.g. increases in species richness, abundance or diversified community composition) are often reported from aquatic environments (Law et al., 2019; Willby et al., 2018), but such aspects are rarely studied beyond the pond.

The connection between a semi-aquatic mammal and terrestrial invertebrate pollinators might, at first sight, seem tenuous. Increasingly, however, it is recognised that the engineering activities of beavers also have profound effects on adjacent terrestrial systems and their biodiversity (Fedyń et al., 2023; Nummi et al., 2019; Orazi et al., 2022). Habitat modification through tree felling and altered vegetation composition could additionally support pollinators if they boost floral resources. Despite the global importance of insect pollinators for pollination (87.5% of flowering plants and approximately 35% of global food production, valued at US$21.5 trillion a year; Klein et al., 2007; Ollerton et al., 2011) and the imperative need to reverse population declines, only two studies have investigated the influence of beaver-modified habitats on pollinators. Bartel et al. (2010) found that the rare St Francis's Satyr *Neonympha mitchellii francisci* butterfly was indirectly supported by beaver engineering as the early successional conditions alter plant composition and diversity. Andersen et al. (2023) studied moth communities and found that species richness and diversity were higher in beaver wetlands compared to surrounding recently clear-felled conifer woodland, most likely due to the habitat disturbances resulting from beaver activity. Habitat modification by beavers might thus support pollinator populations at the local and landscape levels and influence pollination, especially as beaver populations continue to recover from historic range losses and their habitat engineering effects become more widely manifested (Halley & Rosell, 2002).

Human-created ponds are well documented to support diverse pollinator communities, maintain robust plant-pollinator networks, and enhance the delivery of pollination as an ecosystem service (Stewart et al., 2017; Walton et al., 2020, 2021a, 2021b). Pond restoration, by the removal of scrub and coppicing of surrounding trees to increase light and removal of organic matter and sediment, has been demonstrated to benefit diurnal pollinator communities, although nocturnal pollinator communities show an opposing trend (Walton et al., 2020, 2021a). Post-creation or post-restoration related disturbance the banks and margins of other ponds (including human-created ponds) offer relatively stable environments, and their vegetation can often therefore become dominated by competitor and stress-tolerant species (Law et al., 2019) that typically invest in slow growth, often over several seasons to reach a large size with generally lower flower production (Grime, 1977).

In contrast, the margins of beaver wetlands are physically and biologically highly heterogeneous and in a constant state of flux due to fluctuating water levels resulting from dam creation, repair and leakage, removal of canopy cover, extraction of woody debris and selective herbivory (Hyvönen & Nummi, 2008; Willby et al., 2018). This increases plant heterogeneity at varying temporal and spatial scales and facilitates the proliferation of ruderal species (Law et al., 2017, 2019), which are often fast growing and invest heavily in flowering (Grime, 1977). The activity of beavers can therefore alter the composition, structure, diversity and floral traits of plant communities. These factors are known to influence the composition of pollinator communities in other systems (Garrido et al., 2019; Kral-O'Brien et al., 2021). This heterogeneity could also influence plant–pollinator interactions, potentially leading to more specialised networks in beaver wetlands since patchy and changing floral resource availability may reduce the randomness of flower visitation by pollinators, promoting foraging selectivity (Blüthgen et al., 2007).

To our knowledge, no previous study has assessed the influence of beaver-modified ponds on pollinator communities across multiple taxonomic groups and the underlying structure of plant–pollinator interactions. In this study, we address this gap and provide a comparison between beaver wetlands (BW) and human-created ponds (HCP) in a semi-upland agricultural landscape in eastern Scotland. We first examine if the margins of BW support (1) higher plant species richness and (2) distinct plant composition, both being factors known to influence pollinator communities. We then specifically test if (3) BW have higher diurnal pollinator (bees, butterflies, hoverflies and moths) species richness or abundance and identify if floral attributes (number of plants in flower and maximum flower coverage) influence these metrics and (4) if BW support more specialised plant–pollinator interactions at the network level.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was undertaken at six wetlands in eastern Scotland (56°37′32.81″ N, 3°13′36.72″ W, 160–200 m a.s.l.; Figure 1). All wetlands were surrounded by low-density year-round grazing by cattle,

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FIGURE 1 Location of study site in eastern Scotland and sampled wetlands (a, e). Beaver wetland examples (b, c) and human-created pond example (d). Aerial photography © Getmapping Ltd. 2024.

ponies and pigs (<0.11 livestock units per hectare) or wild roe deer. Wetlands themselves were minimally affected by this grazing due to the wetness of adjacent land. Three wetlands were allocated across each of two treatments: (1) BW: hydrologically modified or created by beaver engineering with actively maintained dams and canals and herbivory by beaver; (2) HCP: artificially created, with no evidence of engineering by beavers, but limited grazing by beaver possible due to proximity to BW. HCP all had low surrounding scrub cover and lacked canopy trees.

Wetlands were located 400 m ± 111 m (mean ± SE) apart, with a minimum distance between sites of 205 m (Table S1). Five of the six wetlands were situated along a single stream, with one wetland located just southwest of this catchment (Smiddyhill Pond). HCP were isolated from this stream while BW were connected to the channel. BW were established from 2002 onwards, all being >5 years old, while all HCP had been established prior to 2002.

2.2 | Plant sampling

A total of 15, 1 m^2 quadrats, randomly located around the wetland edge, were surveyed for plants between 17 and 21 July 2023. Percentage cover of each species was estimated to the nearest 5%. Plants were identified to species except ferns which were classed as fern spp. and *Agrostis stolonifera* and *A. canina* which were aggregated due to difficulty of separating mixed stands in the field. One measure of the tallest vegetation plus five random height measures were made to the nearest centimetre in each quadrat. During each pollinator count, the number of plant species in flower and their coverage (using the DAFOR scale) were estimated along the length of the pollinator transect. Flower coverage was then converted to a maximum value by using the species with the highest percentage coverage.

2.3 | Pollinator sampling

Each wetland was visited on six occasions between May and August 2023, with visits 10–25 days apart, dependent on suitable weather conditions. Six visits were undertaken to ensure detection of species with varying seasonality and to ensure coverage of plant–pollinator interactions, whereby certain plants may have short flowering periods. Visual observation surveys intensively sampled all riparian habitat, following a zigzag route

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along the wetland edge, within a sampling width of 5 m and lasting for 30 minutes per wetland. The perimeter of each wetland was walked once during the timed count to avoid double counting of individuals before moving to the next site. Pollinators recorded included butterflies, day flying/easily disturbed by day moths, bees and hoverflies, comprising three taxonomically important pollinator orders of Lepidoptera, Hymenoptera and Diptera. Interactions with flowering plants were noted, that is, when a pollinator species actively engaged (e.g. using proboscis) with the reproductive organ of a plant. All pollinator surveys were undertaken in good weather, with primarily sunny conditions, temperatures >13°C and wind speeds < force 5 on the Beaufort Scale (Pollard, 1977). Individuals were identified to species level wherever possible, but in some instances, genus or family level only was possible. On the day of each pollinator visit, the number of plant species in flower and their coverage (DAFOR scale) were estimated along the length of the pollinator transect. Two categories of land use were calculated using the UKCEH 2023 Landcover map (Morton et al., 2024) around each wetland based on a 500 m buffer. Percentage woodland was calculated by combining broadleaf and conifer woodland. Percentage open habitat consisted of arable and improved grassland combined (though some of these fields have been left fallow since 2021 receiving light grazing). No permits or licenses were required for the fieldwork, but landowner permission was sought. Ethics approval was granted from the Animal Welfare & Ethical Review Body at the University of Stirling (Reference 2023 14057 9628).

2.4 | Data exploration and analyses

To determine if sampling was sufficient for plants, rarefaction curves were generated using iNext with Hill numbers ($q=0$ for species richness) with plant data treated as incidence frequency (Chao et al., 2014; Hsieh et al., 2016) (Figure S1). Plant species richness was tested for normality using a Shapiro–Wilk test and found not to be normally distributed. Therefore, for Hypothesis 1, a generalised linear mixed effect model (GLMM) with Poisson distribution was used to test for differences in plant species richness between the two wetland types. Site identity was included as a random effect to account for potential site-specific effects, and it improved the AIC of the model. To characterise differences in plant composition between wetland types for Hypothesis 2, we carried out an unconstrained ordination using Non-Metric Multidimensional Scaling (NMDS) on a Bray–Curtis dissimilarity index of plant percentage cover with three dimensions ($k=3$) to visualise differences between the wetland types. We tested for statistical differences in community composition, based on the centroid of the hull, using the adonis2 function with 10,000 permutations (Oksanen et al., 2022). Indicator plant species were generated using the Indval function (Roberts et al., 2023) (Table S2). For each indicator species, CSR growth strategies were assigned following (Grime et al., 1988; Pierce et al., 2017) and Ellenberg values for light, moisture and nitrogen following values for British plants in Hill et al. (1999) (Table S2).

Apis mellifera was removed from all pollinator analysis as its occurrence is largely dependent on hive keeping. Rarefaction curves for pollinator species richness using Hill numbers ($q=0$) of each taxonomic group and abundance (number of individuals) were calculated using iNext (Figure S2). Prior to models being constructed to test for differences in species richness between the wetland types, observations not made consistently at the species level were removed (e.g. if *Eristalis* spp. were recorded but then *Eristalis pertinax* was also recorded at that site, only the higher taxonomic resolution was retained). For abundance models, all observations were included. Data were tested for normality using a Shapiro–Wilk test, and neither richness nor abundance datasets were normally distributed. A correlation matrix between the predictor variables (number of plant species in flower per visit, maximum flower coverage, open habitat and woodland covers) was created to check for collinearity amongst explanatory variables. Woodland and open habitat were highly correlated ($r \geq 0.6$), so only open habitat was retained. All other variables had low correlations ($r < 0.42$). For Hypothesis 3, we constructed eight GLMMs, using either richness or abundance summed per visit for each discrete taxonomic group as the response, with wetland type, number of plant species in flower per visit, maximum flower coverage per visit and open habitat cover as the predictor variables, and site as a random effect. The two floral explanatory variables and open habitat cover were scaled to zero mean prior to analysis. Within GLMMs, a Poisson distribution was fitted for hoverfly richness/abundance, bee richness and moth richness, but under- and over-dispersion was detected for all remaining models. When overdispersion was detected, a negative binomial distribution was fitted (bee, butterfly and moth abundance models), and when underdispersion was detected (butterfly richness), the genpois distribution was fitted. All models were run using glmmTMB (Brooks et al., 2017). Richness or abundance were modelled per visit as initial data exploration revealed seasonal effects for some groups, which would be masked by pooling data (Figure S3). All models were checked for multicollinearity using Variance Inflation Factors (VIF's). No high VIFs (>3) were detected (Kock & Lynn, 2012). All model assumptions were checked using the DHARMa package (Hartig, 2022) and AICs in the package Performance (Lüdecke et al., 2021). Spatial autocorrelation was checked using the recalculateResiduals function in the DHARMa package, which accounts for multiple visits to the same site and calculates a Moran's *I* value. Spatial autocorrelation was only detected in the moth richness model (Table S3).

Data were subset into two seasonal blocks for network analysis to reduce the chance of introducing plant–pollinator interactions that are unlikely (e.g. spring flying species interacting with a late summer flowering plant) in subsequent null model analysis (Blüthgen & Staab, 2025). The first block covered visits undertaken in May–June and the second block covered visits undertaken in July–August. Rarefaction curves for plant-pollinator interactions of both networks and seasons were estimated using Hill numbers ($q=0$) (number of links) and abundance (number of flower visits)

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following Devoto et al. (2012) using iNext (Figure S4). Singleton interactions were retained in the analysis as these were considered biologically meaningful while our sampling design based on repeated visits to each site reduced the chance of under-sampling flower patches. The network metric H_2' was selected as this shows the level of specialisation of the entire network (niche partitioning), ranging from 0 (low specialisation) to 1 (high specialisation) (Blüthgen et al., 2006). This metric was selected as it is quantitative, accounting for differences in interaction frequency, has been mathematically analysed and simulated and is comparatively robust to network size and sampling intensity (Blüthgen et al., 2006; Blüthgen & Staab, 2025). To determine whether the degree of specialisation observed in the networks was greater than for randomly assembled networks, we compared each of the four network H_2' values to the Patefield null model using 500 simulations. The Patefield null model preserves the relative abundance of each species and the species richness elements of the model (Blüthgen & Staab, 2025). Subsequently, we tested for the difference in network specialisation between BW and HCP following the methods in Dormann (2024). Initially, we calculated the difference in observed H_2' values of the wetlands (mean of HCP May–June and HCP July–August minus the mean of BW May–June and BW July–August). The difference between the observed H_2' values for the wetland types and 5000 simulations of H_2' using a Patefield null model (Patefield, 1981) were then compared. To generate a p-value, the observed and null model statistics were compared, and the proportion of values exceeding the observed were counted (Dormann, 2024). All data analysis was undertaken using R version 4.3.2 (R Core Team, 2023) and is available in Cook (2025).

3 | RESULTS

3.1 | Plants

A total of 79 plant species were recorded, 59 in BW and 57 in HCP (Tables S4 and S5). Sample completeness was 96.7% in BW and 95.7% for HCP (Figure S1). Species richness per quadrat did not differ significantly between wetland types (Figure S5; Table S6). Both wetlands shared plant species, as shown by their overlapping hulls in ordination space; however, plant composition, represented by the hull centroids, did differ significantly (Figure 2a). Eleven indicator plant species were identified in BW and nine in HCP. Indicator species in BW were predominantly associated with ruderal and competitor growth strategies, whereas in HCP stress tolerators dominated (Figure 2b; Table S2). For Ellenberg scores, indicator species in BW were tolerant of higher shade, moisture and nitrogen (Table S2).

3.2 | Pollinator species richness and abundance

A total of 669 individuals of 54 pollinator species were recorded in BW and 612 individuals of 55 pollinator species were recorded in HCP (Table S4). Sample completeness was consistently high in

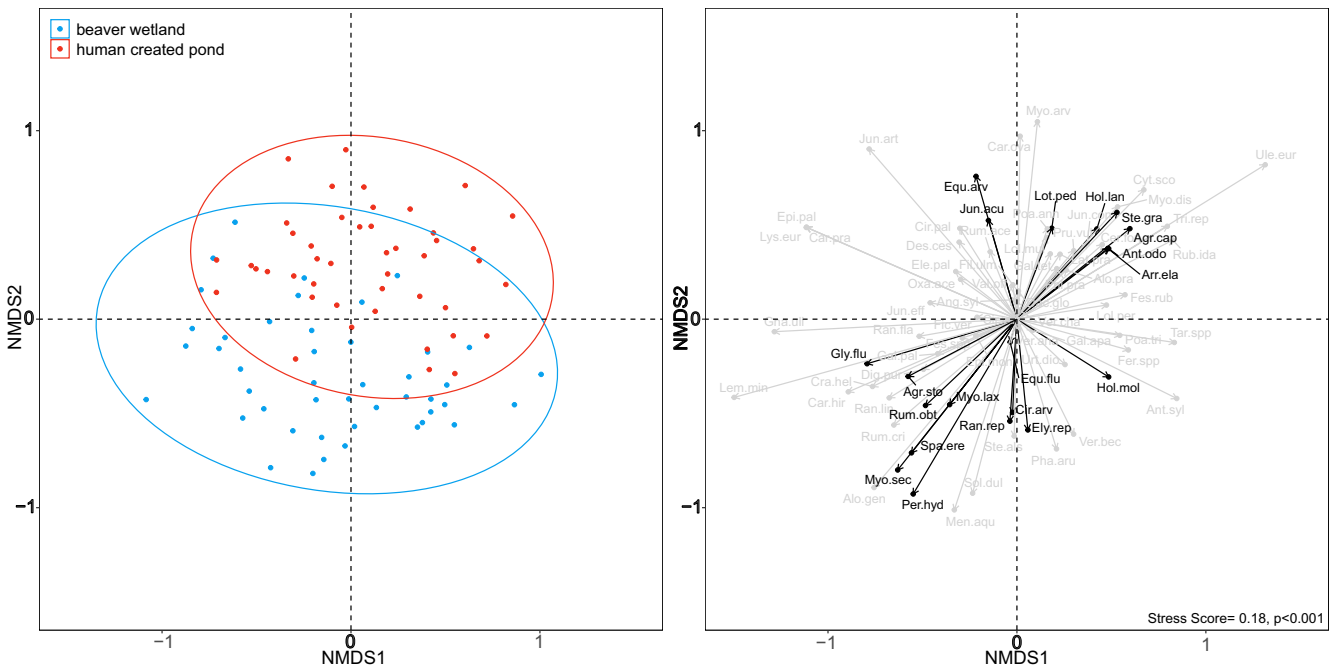

FIGURE 2 Non-metric multidimensional scaling (NMDS) unconstrained ordination plots of plant percentage cover. Left plot shows site scores with ellipses for beaver wetlands (blue circles and ellipsis) and human-created ponds (red circles and ellipsis). Right plot shows species scores with indicator plant species in black and non-indicator plant species in grey. *p*-values represent the output from permutational multivariate analysis of variance.

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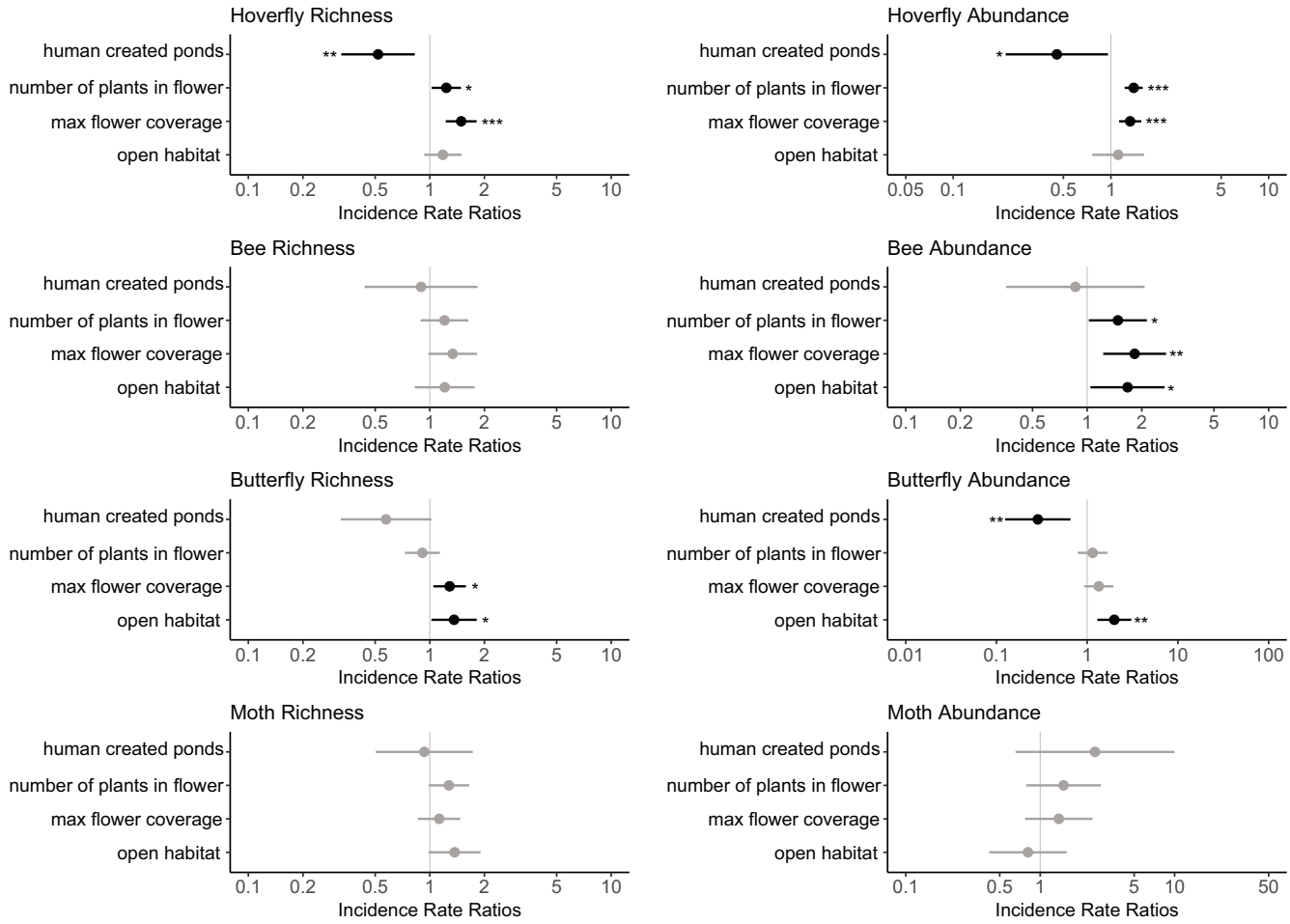

FIGURE 3 Forest plots showing model outputs for species richness and abundance estimates for each taxonomic group between the wetland types and in response to floral characteristics and open habitat. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

both wetland types, hoverflies (BW 96.4%, HCP 95.8%), bees (BW 98.7%, HCP 98.2%), butterflies (BW 97.4%, HCP 98.7%) and moths (BW 98.3%, HCP 97.5%) (Figure S2). Hoverfly richness per visit was significantly higher (+29%) in BW (9.7 species ± 4.5, mean ± SE) than in HCP (7.5 ± 1.9 SE) ($p = 0.006$) and was positively associated with the number of plant species in flower ($p = 0.027$) and maximum flower coverage ($p < 0.001$) (Figure 3; Figure S6; Table S7). Hoverfly abundance per visit was significantly higher (+119%) in BW (17.2 individuals ± 5.0, mean ± SE) than in HCP (7.8 ± 1.3 SE) ($p = 0.038$) and was positively associated with the number of plant species in flower ($p < 0.001$) and maximum flower coverage ($p < 0.001$) (Figure 3; Figure S7; Table S7). Butterfly abundance per visit was significantly higher (+45%) in BW (6.2 individuals ± 1.9 SE) than in HCP (4.3 ± 1.7 SE) ($p = 0.003$) and was positively associated with open habitat cover ($p = 0.001$) (Figure 3; Figure S7; Table S7). No significant effects of wetland type were detected on butterfly richness or on the richness and abundance of bees and moths (Figure 3). Butterfly richness and bee abundance also showed a positive association with maximum flower coverage and open habitat cover, and the latter also with the number of plant species in flower (Figure 3).

3.3 | Plant–pollinator interactions

None of the rarefaction curves completely plateaued, but all showed similar levels of sample completeness for plant–pollinator interactions (BW May–June 71.5%, BW July–August 83.6%, HCP May–June 82.3%, HCP July–August 74.5%). In BW, a total of 336 interactions with plants were recorded from 38 pollinator species (Figure 4; Table S8). Hoverflies were responsible for 60.1% of interactions, with *Episyrphus balteatus* (14.6% of interactions), *Bombus pascorum* (11.9%) and *Eristalis pertinax* (8.0%) being the most frequent interacting pollinators. For BW, *Cirsium arvense* was the most frequently visited plant (28% of interactions), followed by *Ranunculus lingua* (16.4%) and *Valeriana officinalis* (12.2%). In HCP, the total number of interactions was 31% lower (231 interactions), involving 34 pollinator species (Figure 4; Table S8). Bees were the most frequent pollinator, accounting for 42.9% of the interactions, followed by hoverflies (29.9%). *Bombus pascorum* (29.9% of interactions), *Glyptherix simpliciella* (13.0%) and *Bombus terrestris/lucorum* (9.5%) were the most frequent interacting pollinator species. For plants, *C. arvense* (20.8% of interactions) was again the most frequently visited species, followed by *Cirsium palustre* (17.7%) and *Lotus pedunculatus* (13.9%).

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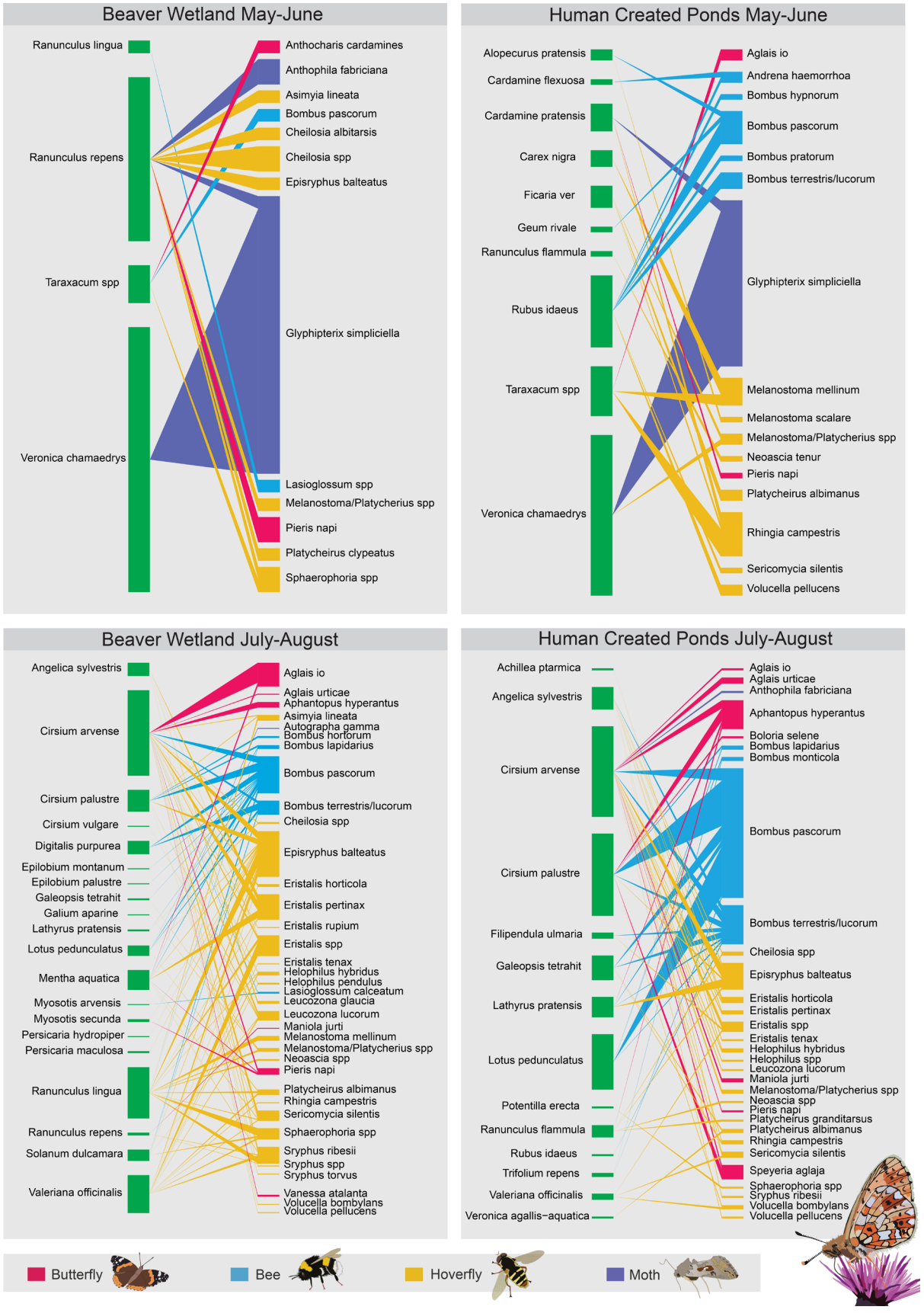

FIGURE 4 Plant–pollinator interaction networks for beaver wetlands May–June (top left), beaver wetland July–August (bottom left), human-created ponds May–June (top right) and human-created ponds July–August (bottom right). The width of the link refers to relative interaction frequency. This width is comparable between wetland types within a season but not across seasons.

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All network specialisation scores were significantly different from the null model, indicating networks were constructed non-randomly (Table S9). Network specialisation scores were higher in the May–June period for both wetland types compared to July–August. Comparison of network specialisation (H_2') between the wetland types found no significant difference ($p = 0.07$, Figure S8).

4 | DISCUSSION

We found that hoverflies and butterflies were 119% and 45% more abundant, and hoverfly richness 29% higher in BW compared to HCP, while bees and moths did not differ between wetland types. Hoverflies are an important but under-appreciated pollinator group (Doyle et al., 2020; Lucas et al., 2018), and butterfly populations are declining rapidly (Fox et al., 2023). Our results therefore emphasise the potential for BW, in tandem with other freshwater habitats, to help reverse pollinator declines at the landscape scale. Currently, national pollinator strategies (e.g. Scottish Government, 2017) rarely mention wetlands as habitat for pollinators (Vasiliev & Greenwood, 2020). Here, we argue that BW explicitly should be considered part of the toolbox of agri-environment schemes and national pollinator strategies and afforded the same privileges as pond margins and riparian buffers to provide a scalable (UK Government, 2023), landscape applicable method to restore pollinators.

4.1 | Pollinator richness and abundance

BW and HCP had similar richness for three taxonomic groups studied and similar abundance of bees and day-flying moths. Other studies have documented the benefits of HCP, particularly open canopy, restored ponds, for pollinators as a semi-natural habitat in agricultural landscapes (Stewart et al., 2017; Walton et al., 2021a, 2021b); here we show that BW can attain a similar number of species and abundance across key pollinator groups but with the added benefit of boosting hoverfly richness and both hoverfly and butterfly numbers. Hoverflies are a widely under-appreciated pollinator group (Doyle et al., 2020) while 80% of UK butterfly species are declining in abundance or distribution (Fox et al., 2023). BW are dynamic and heterogeneous habitats maintained by regular beaver disturbances and water level fluctuations, and thereby differ in their vegetation from other co-occurring wetlands (Willby et al., 2018), even in our study with limited spatial replication. The resulting floral attributes and habitat, as shown in this study, provide breeding and adult foraging resources for hoverflies and butterflies, boosting their abundance, and richness for the former group. For example, shallow, fluctuating water margins with an abundance of decaying organic material provide ideal larval habitat for the hoverfly genera *Eristalis* and *Helophilus* (Stubbs & Falk, 2002). Most of the species in these two genera had higher abundance in BW compared to HCP in this study. Similarly, for butterflies, BW had a higher abundance of species preferring damper conditions, for example, *Anthocharis cardamines*. BW have unique physical characteristics such as an abundance of standing (flooded trees) and fallen deadwood (e.g. dams, caches and lodges) which provides a breeding resource for deadwood-associated species, for example, *Xylota sengis*, and may benefit scarcer deadwood specialists, for example, *Chalcosyrphus eunotus* (Stubbs & Falk, 2002).

BW supported diverse foraging opportunities for hoverflies and butterflies, particularly in late summer (Figure S3), with many of the indicator plant species associated with a ruderal or competitor growth strategy, for example, *C. arvense* and *Ranunculus repens* (Table S2; Grime et al., 1988; Pierce et al., 2017). These plants respond positively to the frequent disturbances introduced by beavers and typically invest in high reproductive output and flower production (Grime, 1977). Flower visitation provides two key benefits to pollinators in the form of nectar as an energy source for flight and pollen as a source of protein to support reproduction (Doyle et al., 2020). BW supported a higher frequency of hoverfly and butterfly flower visits than HCP, as shown by the plant–pollinator interaction network (Figure 4). The trend for the latter group was driven primarily by the interaction between *Aglais io* and *C. arvense*. The provision of floral resources and breeding habitat in BW could increase the resilience of butterflies to environmental change (Montràs-Janer et al., 2024). This can only occur if BW are allowed to develop through favourable policies and will have the greatest benefit when BW occur in open habitat, as shown by the positive association we observed between butterfly abundance and open habitat. This, alongside the positive association with maximum flower coverage for hoverflies, were important factors in increasing the abundance of these two groups compared to HCP (Figure 3; Table S7). Pollinators display diverse morphology (e.g. degree of hairiness or length of proboscis), which can influence flower visitation and thus habitat affinity. For example, hoverflies with a relatively short proboscis, for example, *Episyrphus balteatus*, prefer flat-open flower structures species (e.g. *Valeriana officinalis* and *Ranunculus lingua* in our study), whereas those with a longer proboscis, for example, *Rhingia campestris*, can use flowers with deeper tubes (Gilbert, 1985). The former hoverfly species was 154% more abundant in BW than HCP, whereas the latter was 15% higher in HCP.

The provision of floral resources which support higher hoverfly or butterfly abundance and flower visitation is important as hoverflies in particular are increasingly considered a critical pollinator group (Doyle et al., 2020; Lucas et al., 2018; Rader et al., 2016). Reasons for this include their high frequency of flower visitation, relative abundance compared to other pollinators and their ability to transport pollen long distances (Rader et al., 2011; Wotton et al., 2019). Whilst beyond the focus of our study, increased hoverfly abundance around BW could confer other ecosystem services such as the reduction of aphids by aphid-eating hoverfly species. The potential added value of BW in agricultural areas in this regard requires further exploration (Tenhumberg, 1995; Van Oystaeyen et al., 2022; Wotton et al., 2019).

The limited number of wetlands in our study and their relative proximity, within known movement distances of some species

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(Carvell et al., 2012), could result in individuals utilising both wetland types as a habitat resource, thereby diminishing the effect of wetland type, although spatial autocorrelation was only detected for moth richness and our survey design minimised the risk of double counting. The homogeneity and low connectivity of the surrounding agricultural matrix could also diminish the difference between these wetland types, as specialists or those with lower mobility may have reduced capacity to colonise from the wider regional species pool (Öckinger et al., 2018).

Plant–pollinator interactions were dominated by hoverflies in BW, whereas bees dominated interactions in HCP, indicative of different floral resources. This was particularly noticeable in BW during the late summer when hoverflies were abundant, driven by interactions with later flowering species such as *C. arvense*, *R. lingua* and *V. officinalis*. Despite these anecdotal differences in flower visitation, we found no difference in network-level specialisation (H_2') between the two wetland types, despite both having higher specialisation in May–June due to lower flower availability. The marginal test result might, however, repay further investigation in other landscapes, especially due to our limited study area and close proximity of sites. Our findings, therefore, suggest that the mostly widespread and generalist pollinator species recorded in our study interacted with flowers broadly in accordance with their frequency and in a similar way across both wetland types.

We suggest that future studies should expand on our framework, replicating the design across landscapes of differing heterogeneity, connectivity and land cover types (e.g. biodiverse protected areas to intensive agriculture), and over longer time frames due to the temporally variable nature of BW. This would help disentangle local and landscape-scale habitat effects (e.g. see Kirsch et al., 2024) on pollinator communities and networks in BW. Such studies would help determine where beaver reintroductions could be targeted to optimise benefits to pollinators, information that is critical for informing national pollinator strategies and biodiversity support schemes.

5 | CONCLUSIONS

Beaver wetlands have proven benefits for aquatic biodiversity. Our study, set in a typical semi-upland low-diversity agricultural landscape, shows for the first time that they also boost hoverfly richness/abundance and butterfly abundance, while matching up to human-created ponds for other pollinator groups. Given the increasing recognition of hoverflies in the delivery of pollination services and ongoing declines in butterfly populations, beaver wetlands should therefore be viewed as a scalable nature recovery strategy to reverse pollinator declines by restoring breeding and foraging habitat. Currently, in the United Kingdom, most agri-environment schemes endorse human pond creation, with little financial incentive for landowners to accommodate beaver wetlands on their land, despite the potential boost in pollination services. This position needs to change if we are to benefit from the buzz, flutter and hum of pollinators that beaver wetlands promote.

AUTHOR CONTRIBUTIONS

Patrick Cook, Alan Law, Zarah Pattison and Nigel Willby conceived the idea and designed the methodology; Patrick Cook collected and analysed the data, and led the writing of the manuscript; Patrick Cook, Alan Law, Zarah Pattison and Nigel Willby all contributed to writing and revising the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available on Zenodo https://doi.org/10.5281/zenodo.17279196 (Cook, 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Plant rarefaction curves. Left plot shows sample-sized base curve and right plot shows sample completeness curve. Beaver wetlands are a blue line, other ponds a red line and both wetlands combined an orange line.

Figure S2. Rarefaction curves for all pollinator groups combined, bees, butterflies, hoverflies and moths. Blue lines represent beaver wetlands and red lines represent human created ponds.

Figure S3. Hoverfly abundance per visit (a), bee abundance per visit (b), butterfly abundance per visit (c) and moth abundance per visit (d).

Figure S4. Rarefaction curves for plant–pollinator links.

Figure S5. Plant species richness between the two pond types. Dots represent the richness in individual quadrats.

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Figure S6. Species richness per visit of each taxonomic group between the two wetlands.

Figure S7. Abundance per visit of each taxonomic group between the two wetlands.

Figure S8. Histogram showing observed (vertical red line) difference in H_2' between the two wetland types. The observed difference was not significantly different from the Patefield null models ($n = 5000$).

Table S1. Minimum distance to next nearest pond included in the study.

Table S2. Plant indicator species in the study with CSR category (Grime et al., 1988), CSR percentages (Pierce et al., 2017) and Ellenberg values for light (L), moisture (F) and nitrogen (N) (Hill et al., 1999).

Table S3. Moran's *I* spatial autocorrelation results, variance inflation factor scores and AIC scores for all models. Significant results are highlighted in bold.

Table S4. Richness and abundance (in brackets) of invertebrate taxonomic groups in each wetland type.

Table S5. Plant and invertebrate species recorded at each site. Numbers under site columns for plants represent number of quadrats that species was recorded in. Numbers under site columns for invertebrates represent the abundance of that species.

Table S6. Results from GLMM for plant species richness between the two pond types.

Table S7. Summary table for the influence of pond type on taxonomic group species richness and abundance. Beaver wetlands are the intercept. For statistical significance levels a * indicates a significant *p* value <0.05, ** highly significant *p* value <0.01 and *** very highly significant *p* value <0.001.

Table S8. Number of species involved in flower visits and abundance of flower visits (in brackets) for taxonomic groups between the two wetland types.

Table S9. Network specialisation scores and *p*-values in relation to Patefield null models.

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